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## HISTOMORPHOLOGY OF THE FEMALE REPRODUCTIVE TRACT IN PHYLLOSTOMOID BATS

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Studies on the female reproductive organs of Chiroptera have shown that bats possess an amazing diversity of anatomical and functional specializations compared to other groups of mammals (Rasweiler, 1979a; Wimsatt, 1975, 1979). Bats possess more variation in uterine morphology than any other mammalian order; pteropodids and emballonurids have primitive duplex uteri, whereas bicornuate and simplex uterine morphologies have evolved within other chiropteran families (Mossman, 1977). Despite this diversity in uterine morphology, there has been little synthesis towards a general understanding of the evolution of this complex organ in bats.

Robin (1881) was apparently the first to provide a comparative morphological study of female genitalia in bats. He examined 45 species of 10 currently recognized families and documented the tremendous diversity in the gross morphology of the chiropteran uterus. Although he did not comment extensively on the phylogenetic implications of his findings, Robin suggested that some phylogenetic relationships could be predicted on the basis of uterine morphology. Wood Jones (1917) considered female internal and external genitalia in 19 species of eight currently recognized families. He proposed that several types of uteri are found among families of bats. The duplex uteri of pteropodids and the highly fused uteri of phyllostomids (including mormoopids) were established as unique extremes among these types. Although the duplex uterus of pteropodids is distinct compared to that found in most other bat families, it is apparently a primitive uterine mor-

phology and, as such, does little to resolve phylogenetic relationships among bats. On the other hand, the uteri of the New World families Noctilionidae, Mormoopidae, and Phyllostomidae appear to be uniquely derived among bats. If the highly fused uterus of these chiropteran families represents a shared-derived feature, then it predicts a close phylogenetic relationship for noctilionids, mormoopids, and phyllostomids.

The systematic relationships of noctilionids, mormoopids, and phyllostomids have been studied extensively in recent years. Several independent data sets suggest that these bats share uniquely derived features that indicate close phylogenetic relationships (Walton and Walton, 1968; Smith, 1972, 1976; Patton and Baker, 1978; Luckett, 1980). On the basis of these shared-derived features, recent authors have regarded noctilionids, mormoopids, and phyllostomids as members of a monophyletic group, and have placed them in the superfamily Phyllostomoidea (for use of superfamilial and familial names, see Handley, 1980).

The present paper reports the results of a comparative histomorphological study of the uterus, oviducts, and ovaries in the New World families Noctilionidae, Mormoopidae, and Phyllostomidae. The reproductive biology of noctilionids and phyllostomids has been well studied in only six genera, including *Noctilio* (Anderson and Wimsatt, 1963; Rasweiler, 1977, 1978), *Desmodus* (Wimsatt, 1954; Wimsatt and Trapido, 1952; Quintero and Rasweiler, 1974), *Macrotus* (Bradshaw, 1962; Bodley, 1974; Bleier, 1975) *Glossophaga* (Hamlett, 1935; Rasweiler, 1972, 1974, 1979b), *Carollia* (Bonilla and Rasweiler, 1974), and *Artibeus* (Wislocki and Fawcett, 1941; Tamsitt and Valdivieso, 1963, 1965; Fleming, 1971). Virtually no information exists on the reproductive biology of mormoopids (Wimsatt, 1979).

The purpose of this paper is to present a comparative data set on reproductive histomorphology of phyllostomoid bats. It is hoped that this study will provide a stimulus for future research on the reproductive biology of individual species. In addition, because phylogenetic relationships of these three families have been well studied through several independent data sets, the usefulness of female reproductive histomorphology in testing phylogenetic hypotheses can be assessed. Phylogenetic implications are treated in detail elsewhere (Hood and Smith, 1982).

## Materials and Methods

Specimens used in this study were obtained from natural populations. Whole female reproductive tracts were excised, then fixed in Zenker's or Bouin's solution

(Humason, 1972). Reproductive tracts also were removed from formalin-fixed museum specimens. The quality of fixation in this latter material varied greatly; in many cases only general anatomical relationships could be ascertained. The reproductive status of individuals used in this study included most stages of the female cycle. Many specimens had early-implanted blastocysts, although some late-pregnant uteri also were examined. The former condition is especially informative regarding oviductal histomorphology and in defining sites of implantation (Rasweiler, 1977, 1979a). Specimens in later stages of pregnancy were less useful in describing uterine morphology because of displacement or destruction of tissues by the developing embryo.

## Histological Procedures

Tissues were processed through paraffin, serially sectioned at 6-8 micra, and stained with Mallory's Trichrome (Humason, 1972) or Gomori's One Step Trichrome Method (Thompson, 1966:788). The Gomori Trichrome staining method is capable of discriminating epithelial, connective, muscular, and vascular tissues and has been applied to the study of complex organs (Bhatnagar and Kallen, 1974; Bhatnagar, 1980; Smith and Madkour, 1980). Organization of connective tissues is especially well demonstrated by the light green component of the stain, a feature important for detailing oviductal penetration into the uterus (see Rasweiler, 1974, for a similar discussion concerning Masson's Trichrome). One modification of the Gomori Method was found to improve our results. The standard treatment with hot Bouin's solution (56°C) for one hour frequently led to sections loosening from the slides. This undesirable effect was remedied by substituting this treatment with 12 to 18 hours in room temperature (20°C) Bouin's solution; staining intensity was maintained with excellent clarity.

Most of the reproductive tracts were sectioned in the frontal plane although a few were prepared in transverse section. Reconstruction of the histomorphology of the female reproductive organs was accomplished by examination of serial sections. Each reproductive tract, so examined, was compared to photographs and or drawings taken before the specimen was prepared histologically.

## Out-group Comparison and Phylogenetic Characters

One of the goals of comparative studies is to present primary descriptive accounts that can be used to assess phylogenetic relationships. A logical framework for the testing of phylogenetic hypotheses has been presented by Hennig (1966) and discussed by Smith (1980). Luckett (1980) has emphasized three important aspects of phylogenetic character analysis. These include: 1) determining the homologous or homoplastic nature of shared similarities among organisms; 2) identifying and arranging character states into transformation series; and 3) determining the relative primitive or derived nature of these character states.

In the present paper, histomorphological features are described and are hypothesized as primitive (plesiomorphic) or derived (apomorphic) on the basis of the out-group comparison method (Watrous and Wheeler, 1981). This will provide a basis for subsequent cladistic analyses. Representatives from the following chiropteran families were examined as out-groups to noctilionids, mormoopids, and phyllostomids: Pteropodidae, Emballonuridae, Rhinolophidae, Hipposideridae, Vespertilionidae, Mystacinidae, and Molossidae. Literature reports were used to determine character distributions in other eutherian orders.

## Specimens Examined

Reproductive tracts (116) of the following taxa were examined (numbers in parentheses indicate sample size): PTEROPODIDAE: *Rousettus amplexicaudatus* (2); *Nyctimene albiventer* (2); *Eonycteris spelaea* (2); *Macroglossus lagochilus* (2); *M. minimus* (2); EMBALLONURIDAE: *Rhynchonycteris naso* (1); *Balantiopteryx plicata* (2); *Taphozous longimanus* (1); *Saccopteryx bilineata* (3); RHINOLOPHIDAE: *Rhinolophus denti* (1); HIPPOSIDERIDAE: *Hipposideros caffer* (1); *H. diadema* (2); NOCTILIONIDAE: *Noctilio albiventris* (3); *N. leporinus* (1); MORMOOPIDAE: *Pteronotus macleayi* (2); *P. parnellii* (6); *P. quadridens* (3); *Mormoops blainvillii* (1); PHYLLOSTOMIDAE: (Phyllostominae) *Micronycteris hirsutus* (1); *M. megalotis* (1); *Macrotus californicus* (4); *Phyllostomus discolor* (4); *P. hastatus* (1); *Phylloderma stenops* (1); *Trachops cirrhosus* (1); (Glossophaginae) *Glossophaga soricina* (3); *Monophyllus redmani* (1); *Leptonycteris curasoae* (2); *Lonchophylla robusta* (2); *Anoura geoffroyi* (1); (Carolliinae) *Carollia castanea* (1); *C. perspicillata* (3); *C. subrufa* (1); *Rhinophylla pumilio* (3); (Stenoderminae) *Sturnira lilium* (4); *Uroderma bilobatum* (2); *Vampyrops helleri* (2); *Vampyrodes caraccioli* (1); *Vampyressa pusilla* (3); *Ectophylla alba* (1); *Artibeus jamaicensis* (4); *Enchisthenes hartii* (1); *Ariteus flavescens* (1); *Ametrida centurio* (1); *Centurio senex* (2); (Brachyphyllinae) *Brachyphylla cavernarum* (1); *Phyllonycteris aphylla* (3); (Desmodontinae) *Desmodus rotundus* (2); VESPERTILIONIDAE: *Myotis adversus* (1); *M. californicus* (2); *M. evotis* (2); *M. emarginatus* (1); *M. lucifugus* (1); *Pizonyx vivesi* (1); *Pipistrellus hesperus* (3); *Rhogeessa tumida* (1); *Scotophilus kuhlii* (1); *Plecotus townsendii* (1); *Antrozous pallidus* (1); MYSTACINIDAE: *Mystacina tuberculata* (2); MOLOSSIDAE: *Tadarida braziliensis* (1); *T. plicata* (1); *Eumops trumbulli* (1); *Molossus molossus* (1).

## UTERINE HISTOMORPHOLOGY

### General Description

The mammalian uterus is a complex, tubular organ which varies considerably in gross morphology. The primitive eutherian uterus is hypothesized to have consisted of two uterine horns (cornua); these open independently into the vagina (Mossman, 1977). Some members of the Chiroptera (see below), Dermoptera, Lagomorpha, and Rodentia have retained this primitive arrangement, whereas derived uterine morphologies have evolved independently in many mammalian orders. Derived morphologies apparently have developed by progressive, caudal to cranial fusion of the uterine horns resulting in the formation of a median, common uterine body. This progression involves two aspects of the uterine horns: 1) superficial tissues of the cornua fuse, and 2) following this external fusion, the internal uterine lumina may become confluent by degeneration of the median septum. However, it is possible that the internal uterine anatomy may be retained in a relatively primitive separated condition despite external fusion of the uterine cornua.

On the basis of gross morphology, both primitive and derived uteri are found within the Chiroptera. All chiropteran families examined in this study (except phyllostomoids) have relatively long uterine horns and moderately short, common uterine bodies. In contrast, the uteri of noctilionids, mormoopids, and phyllostomids have short uterine horns and a prominent, common uterine body; most phyllostomids have a completely simplex uterus.

The mammalian uterus is composed of three histologically well-defined tissue layers. An outer serosa is continuous with the peritoneum and, together with associated mesenteries and ligaments (broad, round, and suspensory), supports the uterus. The thick, middle tunic (myometrium) is comprised of smooth muscle fibers; this layer constitutes a large portion of the uterine wall. The innermost layer (endometrium) is a mucosa of simple columnar epithelium with associated glands, supported by an underlying connective tissue (lamina propria). The endometrium undergoes marked cyclic changes during reproduction. The caudal end of the uterus constitutes the cervix; this region has a distinct mucus-secreting epithelium and a dense connective tissue stroma. Cervical histomorphology has been discussed at length in a number of mammalian orders, including primates, rodents, carnivores, and artiodactyls (Hafez and Jaszczak, 1972; Hafez, 1973a; Graham, 1973; Kanagawa and Hafez, 1973). Caudally, the cervix projects into the vagina as a rounded or conical mound—the portio vaginalis. The cervicovaginal junction is abrupt in most mammals, but varies considerably within primates and bats (Graham, 1973; this study).

In all chiropteran families examined in this study, the free uterine horns were comprised of well-defined myometrium and endometrium; these uterine tissues constitute the gestational portion of the uterus. On the other hand, the common uterine body is comprised of two histologically distinct regions. These include an endometrial-lined gestational portion and the cervix. In the pteropodids and emballonurids examined in this study, the common uterine body is extremely short. The cervix constitutes most of this externally fused portion, whereas only a small amount of the gestational uterus is involved. In all other chiropteran families examined (except phyllostomoids), the common uterine body is longer, but, nonetheless, it is mostly comprised of cervical tissue (Fig. 1). However, in noctilionids, mormoopids, and phyllostomids, the common uterine body is extremely large; the gestational uterus constitutes a major portion, whereas the cervix is limited to
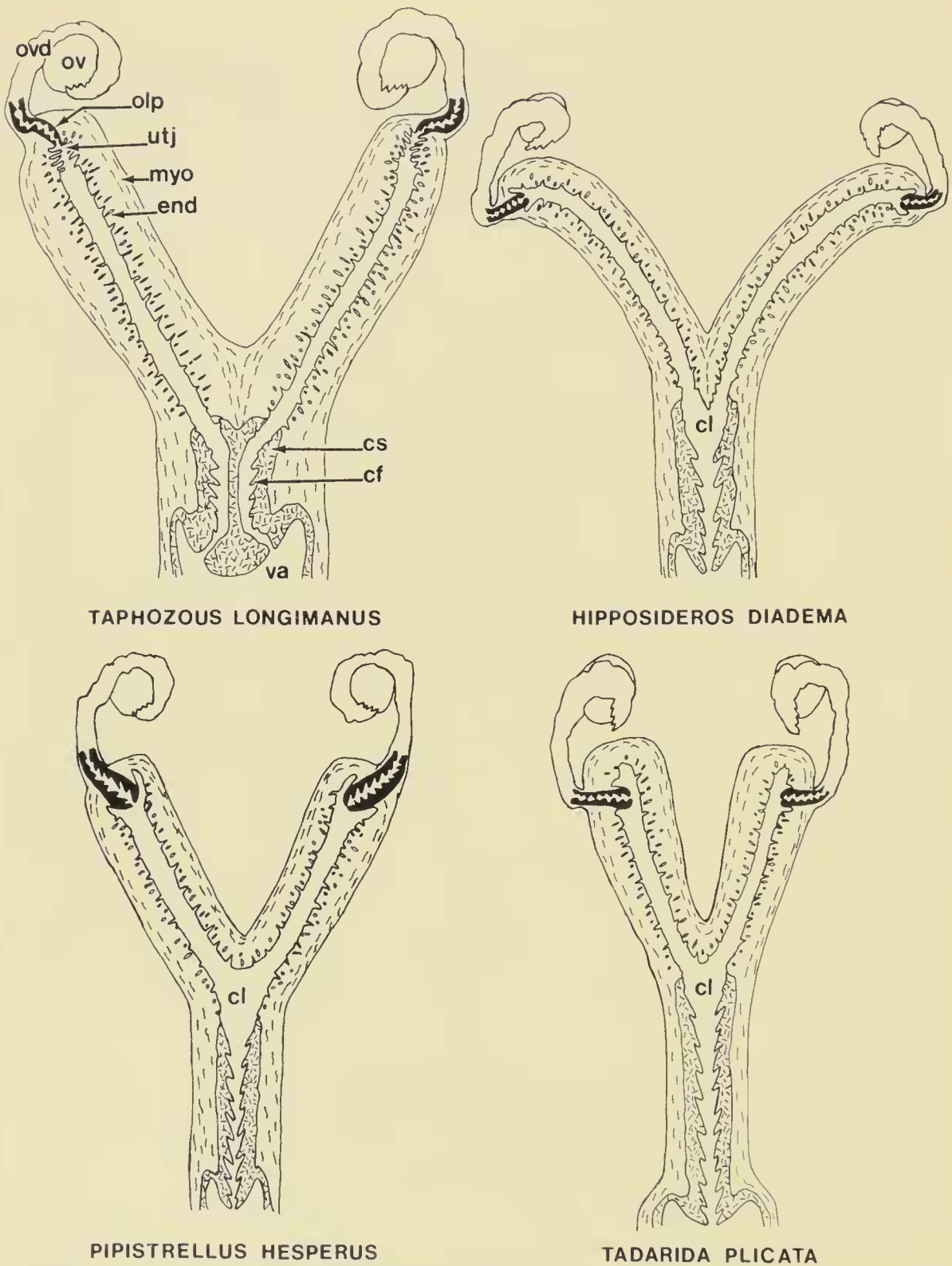
TAPHOZOUS LONGIMANUS

HIPPOSIDEROS DIADEMA

PIPISTRELLUS HESPERUS

TADARIDA PLICATA

Fig. 1.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries of representative chiropteran families, including Emballonuridae: *Taphozous longimanus*; Hipposideridae: *Hipposideros diadema*; Vespertilionidae: *Pipistrellus hesperus*; Molossidae: *Tadarida plicata*. The oviductal lamina propria is shaded to outline the oviduct as it contacts and enters the uterus and to indicate the depth of penetration of the intramural junctura. *Abbreviations:* **ov**, ovary; **ovd**, oviduct; **olp**, oviductal lamina propria; **utj**, uterotubal junction; **myo**, myometrium; **end**, endometrium; **cs**, cervical stroma; **cf**, cervical folds; **va**, vagina; **cl**, common uterine lumen.

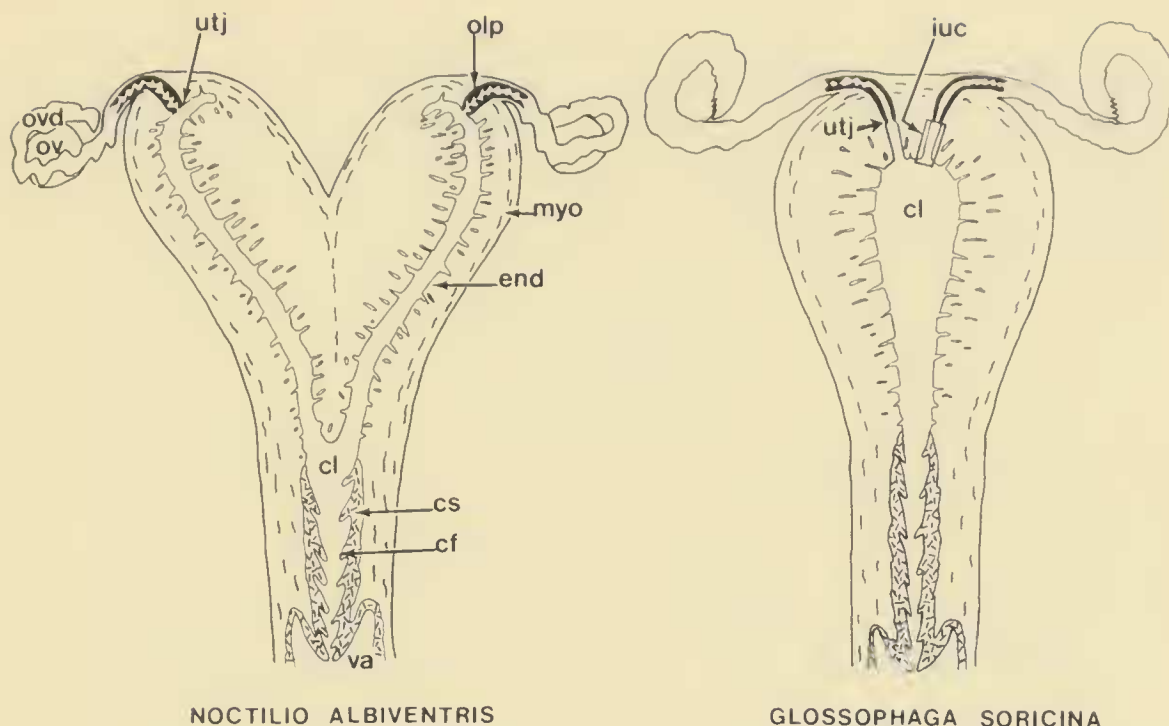NOCTILIO ALBIVENTRIS                    GLOSSOPHAGA SORICINA

Fig. 2.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries of phyllostomoid bats. *Noctilio albiventris* represents phyllostomoids that have a bicornuate uterus, whereas *Glossophaga soricina* is representative of phyllostomoids with a simplex uterus. The presence of tubular, intramural uterine cornua (**iuc**) is a unique feature of the phyllostomoid simplex uterus. Abbreviations can be found in Fig. 1.

the caudal end of the uterus (Fig. 2). This external uterine anatomy, and predominately gestational common uterine body, is considered a shared-derived (synapomorphic) feature of phyllostomoid bats.

Cervical histomorphology of phyllostomoid bats is typical by eutherian standards; the cervical canal has a distinct mucous-secreting epithelium which is thrown into prominent cervical folds. All phyllostomoid bats have a rounded or conical portio vaginalis and a clearly defined cervicovaginal junction.

Internally, all pteropodids examined to date and *Taphozous longimanus* (family Emballonuridae) have completely separate uterine lumina; these have two cervical openings into the vagina (Fig. 1). In all other chiropteran taxa examined, the uterine lumina join within the common uterine body forming a single canal and cervical opening. In the emballonurids *Rhynchonycteris*, *Balantiopteryx*, and *Saccopteryx*, rhinolophids, hipposiderids, and *Mystacina* (family Mystacinidae), this common uterine lumen is limited to the cervix, whereas in vespertilionids and molossids there is a short portion which is lined with gestational uterine tissue (Fig. 1).
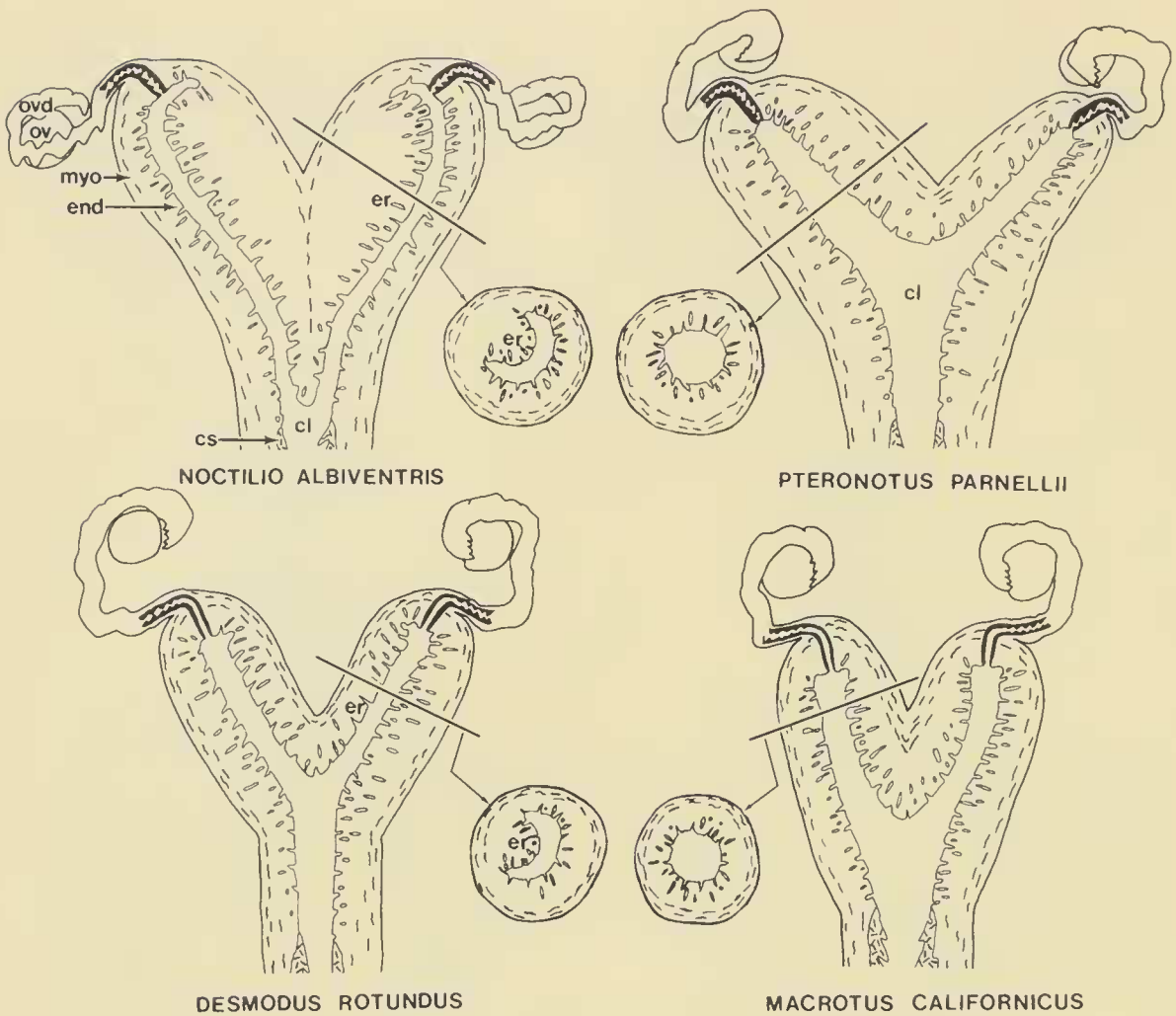
FIG. 3.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative bicornuate phyllostomoids, including Noctilionidae: *Noctilio albiventris*; Mormoopidae: *Pteronotus parnellii*; Desmodontinae: *Desmodus rotundus*; Phyllostominae: *Macrotus californicus*. A unique feature of *Noctilio* and *Desmodus* is the presence of an endometrial ridge (er) in the antimesometrial walls of the uterine cornua. Abbreviations can be found in Fig. 1.

Among phyllostomoid bats, noctilionids have retained markedly separate uterine lumina (Fig. 2). This internal uterine anatomy is similar to that of several chiropteran out-groups (see especially vespertilionids and molossids) and is considered a retained primitive (plesiomorphic) feature for phyllostomoids. On the other hand, the internal uterine anatomy in mormoopids and phyllostomids consists of a large endometrial-lined common uterine lumen; this fused internal anatomy is herein considered a synapomorphy of these two families (Fig. 3). In the systematic accounts that follow, variations in external and internal uterine anatomy among phyllostomoid bats are considered.

## Family Noctilionidae

This Neotropical bat family includes those bats that are referred to as the bull-dog bats or fishing bats. It includes two species in one genus, *Noctilio* (Corbet and Hill, 1980).

The uterus of *Noctilio albiventris* has been described in detail by Anderson and Wimsatt (1963) and we confirm their results. The uterine cornua are short and bulbous, with a prominent common uterine body. Internally, the uterine lumina are not fused throughout the entire length of the common body. An extremely short common lumen is formed just cranial to the cervix. Anderson and Wimsatt (1963) noted that a ridge exists in the antimesometrial walls of the cornua; these ridges serve as sites of implantation (Fig. 3; Rasweiler, 1978, 1979a). It will be noted below that endometrial ridges are also found in the vampire bat, *Desmodus rotundus*.

The one specimen of *Noctilio leporinus* examined in this study had histomorphological features identical to that described above for *N. albiventris*. This specimen possessed an early-implanted blastocyst near the cranial end of an endometrial ridge. This site of implantation is similar to that observed in *N. albiventris*.

In noctilionids, the degree of fusion of the external uterine horns is shared with mormoopids and *Desmodus*. Other phyllostomids have uterine morphologies that are further specialized. On the other hand, the relatively separate internal uterine anatomy of *Noctilio* is shared with other chiropteran families examined herein.

## Family Mormoopidae

The bats of this family are called moustached, naked-backed, or ghost-faced bats. These include two genera (*Pteronotus* and *Mormoops*) and eight species; all live in the Neotropics (Smith, 1972).

The uterine histomorphology of this family has not been described previously. Externally, both *Pteronotus* and *Mormoops* have relatively short uterine horns and a prominent common uterine body (Fig. 3). The cornua are markedly asymmetrical, the right side being anatomically and physiologically hypertrophied (Wimsatt, 1979:346, table 1; this study). The enlarged right uterine horn is similar in size and shape to both symmetrical horns of *Noctilio* (Fig. 3).

Unlike noctilionids, the internal uterine lumina are fused throughout most of the length of the common uterine body forming a large common lumen. In one specimen of *Pteronotus par-*

*nellii*, an early-implanted blastocyst was found in the cranial end of the right cornua. The blastocyst was implanted in the anti-mesometrial wall; however, orientation of the embryonic mass was not determined. Endometrial ridges were not noted in either horn of any mormoopid examined (Fig. 3).

## Family Phyllostomidae

Bats of this family are referred to as New World leaf-nosed bats. This is an especially diverse family, including six subfamilies, 49 genera, and 143 species. All live in the New World tropics and subtropics (Jones and Carter, 1976).

Uterine morphology in phyllostomids is extremely diverse and illustrates progressive fusion of both external and internal uterine anatomy. Patterns of variation in phyllostomid subfamilies are considered in detail below.

*Subfamily Desmodontinae.*—This subfamily includes the true vampires; three monotypic genera include *Desmodus*, *Diaemus*, and *Diphylla*. Anatomical and behavioral adaptations for sanguivory (blood feeding) have led many researchers to regard the vampires as a separate and distinct family, albeit related to phyllostomids. However, this and other recent studies suggest that these bats are within the context of the Phyllostomidae (Machado-Allison, 1967; Forman *et al.*, 1968; Smith, 1972).

The reproductive biology of *Desmodus rotundus* has been studied extensively (Wimsatt, 1954; Wimsatt and Trapido, 1952; Quintero and Rasweiler, 1974). Compared to other phyllostomids, the uterine histomorphology of desmodontines is primitive. Externally, the uterus of *Desmodus* has short uterine horns and a long, common uterine body (Fig. 3). The cornua are symmetrical and tubular, and join to form a common uterine body which is only as wide as either horn. Overall, this uterus is distinctly Y-shaped.

The internal uterine lumina join immediately within the common uterine body forming a large common lumen. This internal anatomy agrees with that described above for mormoopids. A low endometrial ridge exists in the antimesometrial walls of the cornua (Fig. 3); as in *Noctilio*, these ridges serve as a site of implantation (Quintero and Rasweiler, 1974).

*Subfamily Phyllostominae.*—This subfamily includes bats that are known as big-eared, round-eared, sword-nosed, and spear-nosed bats. It includes 11 genera and 34 species that are widely distributed in the New World tropics and subtropics.

Based on uterine histomorphology, members of this subfamily can be arranged in two distinct groups. *Macrotus californicus*, *Micronycteris hirsutus*, *M. megalotis*, and *Trachops cirrhosus* possess uteri with extremely short cornua and a prominent, common uterine body; these taxa are herein referred to as the *Macrotus*-group (Fig. 3). Compared to other bicornuate phyllostomoids (i.e., noctilionids, mormoopids, and *Desmodus*), the external cornua are additionally fused. This external uterine anatomy is considered a synapomorphy of the *Macrotus*-group and other phyllostomids exclusive of *Desmodus*. Internally, the uterine lumina join to form a large common uterine lumen; internal uterine anatomy is similar to that observed in mormoopids and *Desmodus* (Fig. 3).

Anatomical and physiological asymmetry has been noted in *Macrotus* by Bradshaw (1962) and Bleier (1975); the right uterine horn is dominant. In all *Macrotus californicus* examined in the present study, this asymmetry was noted. Although several uteri from subadult individuals were symmetrical in shape, all adult uteri had hypertrophied right cornua. Uteri of *Micronycteris* and *Trachops* examined in this study were identical to pregnant and/or nonpregnant uteri of *Macrotus*.

In contrast to the *Macrotus*-group, the uteri of *Phyllostomus discolor*, *P. hastatus*, and *Phylloderma stenops* are externally simplex; these taxa are herein referred to as the *Phyllostomus*-group. Members of the *Phyllostomus*-group have externally simplex uteri with a tubular- to pear-shaped form (Fig. 4). The fundus of the uterus is prominent and rounded. The simplex uterus is regarded as the most highly derived external uterine anatomy among phyllostomoids.

The internal uterine anatomy of the *Phyllostomus*-group consists of a large common lumen and narrow tubular segments. These tubular segments are actually extremely short uterine lumina and constitute the intramural uterine cornua (IUC; Fig. 4). In one specimen of *Phyllostomus discolor* we discovered an early-implanted blastocyst in an IUC (Fig. 5).

Virtually nothing is known concerning uterine histomorphology in *Phylloderma stenops* (Wilson, 1979). The uterus of one specimen examined in this study was reproductively inactive. Uterine histomorphology of this species was identical to *Phyllostomus*.
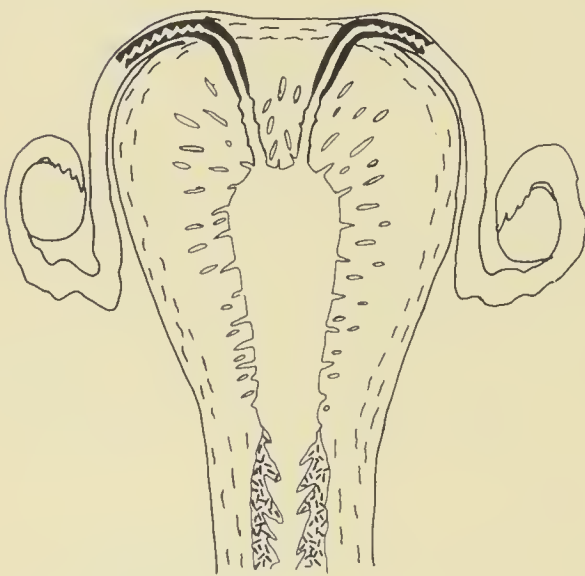
*Subfamily Glossophaginae.*—Bats of this subfamily are referred to as the long-tongued or long-nosed bats. As their name implies,
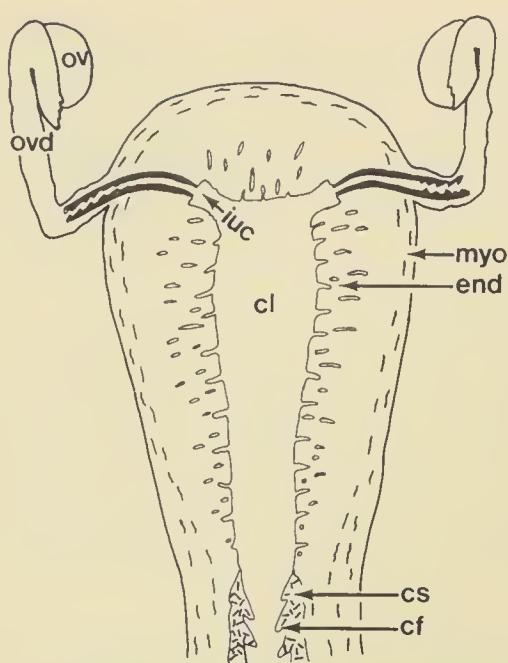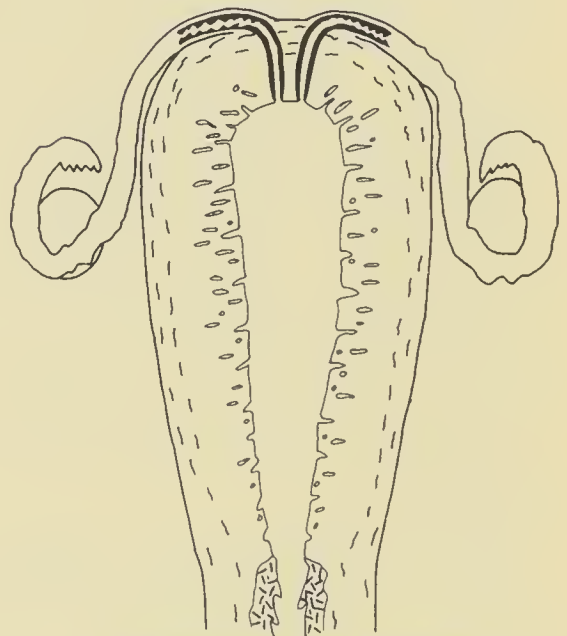
PHYLLOSTOMUS DISCOLOR
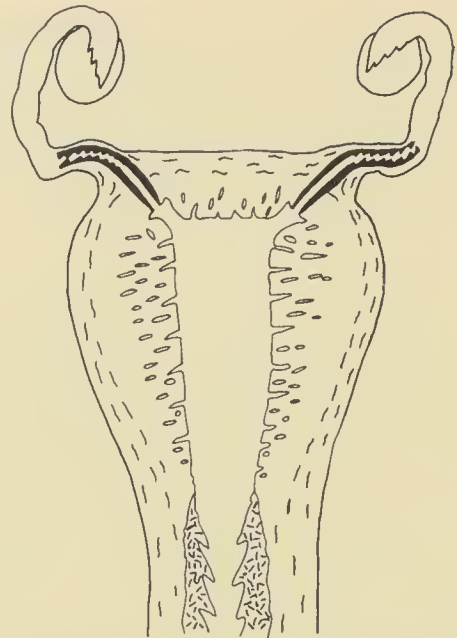
PHYLLONYCTERIS APHYLLA

CAROLLIA PERSPICILLATA

ARTIBEUS JAMAICENSIS

FIG. 4.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative simplex phyllostomoids, including Phyllostominae: *Phyllostomus discolor*; Brachyphyllinae: *Phyllonycteris aphylla*; Carolliinae: *Carollia perspicullata*; Stenoderminae: *Artibeus jamaicensis*. The intramural uterine cornua (**iuc**) is a unique feature of the phyllostomoid simplex uterus. Abbreviations can be found in Fig. 1.

they have highly specialized, elongated muzzles. This subfamily consists of 13 genera and 32 species that live in the New World tropics and subtropics.

All members of this subfamily have externally simplex uteri (Fig. 5). Although some variation exists between genera, glosso-
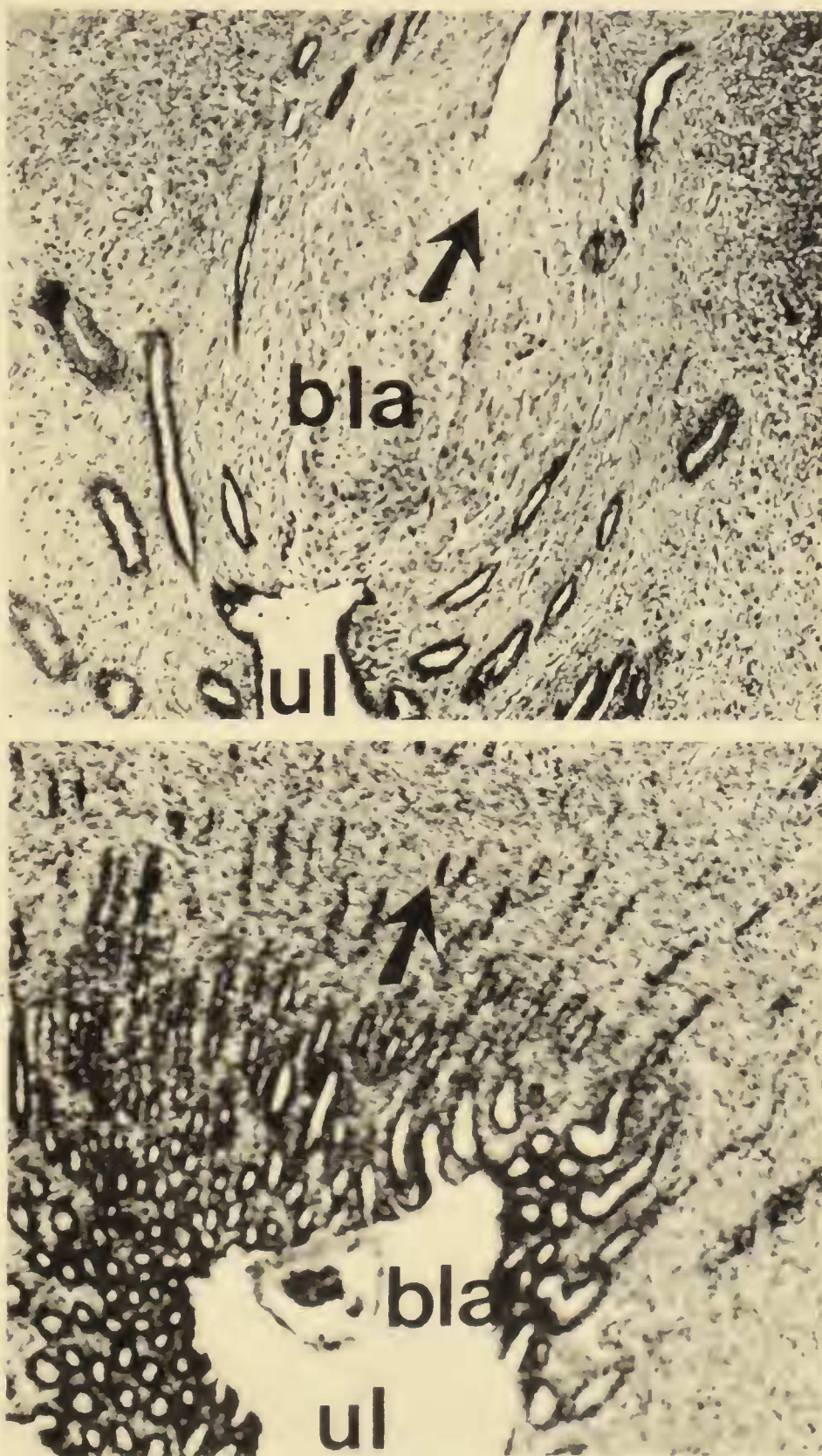
FIG. 5.—Initial sites of implantation and orientation of blastocysts in *Anoura geoffroyi* (*top*) and *Phyllostomus discolor* (*bottom*). In both specimens, blastocysts were implanted in the intramural uterine cornua and the inner cell mass was oriented towards the uterotubal junction of the oviduct ipsilateral to the developing corpus luteum. *Abbreviations:* ul, uterine lumen; bla, blastocyst; arrows in both photomicrographs indicate orientation towards the oviduct. Both 416×.

phagines have a distinctly barrel- to pear-shaped uterus. The fundus was notably flattened in all taxa examined. Internally, glossophagines have a large, common uterine lumen and tubular IUCs. The IUCs are short and broad in *Lonchophylla and Leptonycteris*, but longer in *Glossophaga, Monophyllus*, and *Anoura* (Fig. 6). Rasweiler (1974) has done extensive studies on the form and function of IUCs in *Glossophaga soricina* and noted that initial implantation always occurs in them. Likewise, we discovered an early-implanted blastocyst in an IUC of a specimen of *Anoura geoffroyi* (Fig. 5). Furthermore, in preovulatory specimens of *Leptonycteris* and *Monophyllus*, the endometrial lining of the IUCs was preferentially proliferating compared to that of the common lumen. These data suggest that IUCs function as the primary sites of implantation in all glossophagines.

*Subfamily Brachyphyllinae.*—This subfamily includes those bats referred to as the flower-bats. It contains three genera and seven species, all of which live in the West Indies. The systematics of this subfamily have been discussed by Baker and Bass (1979) (see Baker, 1979, for justification for using the name Brachyphyllinae rather than Phyllonycterinae). Uterine histomorphology in brachyphyllines agrees in all qualitative respects with that observed in the Glossophaginae (Figs. 4, 6). In both *Brachyphylla* and *Phyllonycteris* the uterus is externally simplex and barrel- to pear-shaped. The fundus is flattened and not prominent.

The internal uterine anatomy of *Phyllonycteris aphylla* includes a large, common lumen and short IUCs. These IUCs are oriented towards the latero-fundic border, an arrangement similar to that found in *Lonchophylla* and *Leptonycteris*. Although none of the *P. aphylla* examined had implanted blastocysts, all uteri had moderately to greatly proliferating endometrium lining the IUCs. These observations suggest that IUCs in *Phyllonycteris* function as in other phyllostomids with simplex uteri.

The one specimen of *Brachyphylla cavernarum* examined in this study possessed a large embryo. Unfortunately, invasion of embryonic tissues into the fundus of the uterus was so extensive that some uterine features could not be determined. Although IUCs were not observed, the oviducts descended from the latero-fundic border as in *Phyllonycteris*. Additional uteri of *Brachyphylla* could be profitably studied; presence of functional IUCs would be predicted based on their occurrence in *Phyllonycteris*.

*Subfamily Carolliinae.*— Bats of this subfamily are called short-tailed, leaf-nosed bats. These include two genera (*Carollia* and *Rhinophylla*) and eight species; all live in the Neotropics.
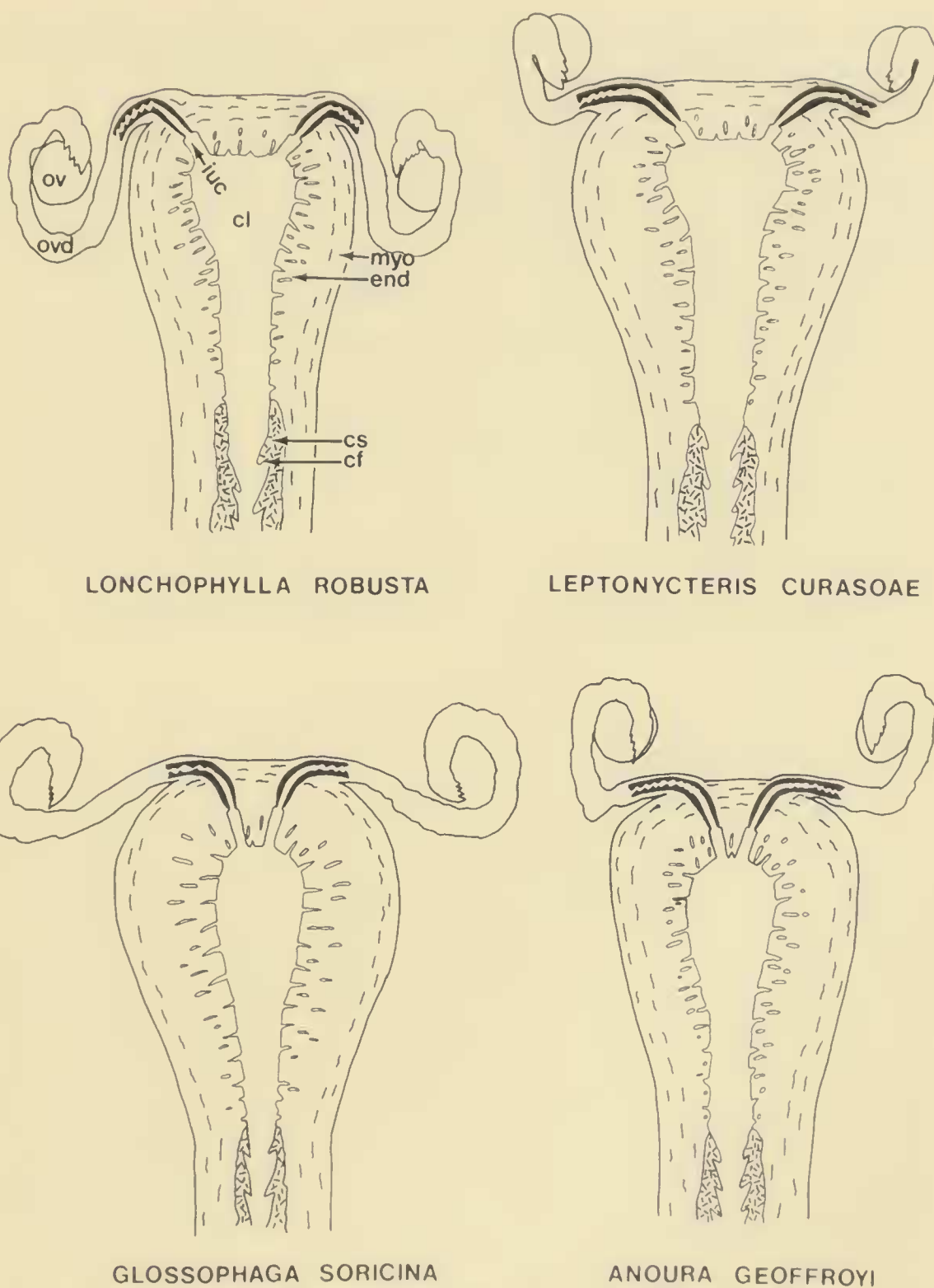
LONCHOPHYLLA ROBUSTA                LEPTONYCTERIS CURASOAE

GLOSSOPHAGA SORICINA                ANOURA GEOFFROYI

FIG. 6.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative Glossophaginae, including *Lonchophylla robusta*, *Leptonycteris curasoae*, *Glossophaga soricina*, *Anoura geoffroyi*. Abbreviations can be found in Fig. 1.

Both *Carollia* and *Rhinophylla* have externally simplex uteri (Fig. 4). Bonilla and Rasweiler (1974) did extensive studies on uterine and oviductal histomorphology in *Carollia*. All species of *Carollia* examined in the present study had broadly pear-shaped uteri. The internal uterine anatomy includes a large, common

lumen and long, tubular IUCs. We observed that blastocyst implantation occurs in the IUCs as in *Glossophaga soricina* (see also Bonilla and Rasweiler, 1974; Rasweiler, 1972, 1979*a*).

In contrast to *Carollia*, the uterus of *Rhinophylla pumilio* is less pear-shaped and more tubular in form. Internally, the uterus has a large, common lumen and short IUCs. No data were available regarding the function of IUCs as a site of implantation.

*Subfamily Stenoderminae.*—This subfamily includes those bats referred to as the New World fruit-eating bats. It includes 17 genera and 60 species. Although taxonomically diverse, stenodermines are a rather homogeneous group. Bats of the genus *Sturnira* have been considered a separate subfamily by some authors; however, recent workers regard this genus as a member of the Stenoderminae (Jones and Carter, 1976; Baker *et al.*, 1979). All stenodermines have distinctly tubular, simplex uteri (Figs. 4, 7). The fundic end of the uterus is covered by the oviducts which enter the uterine body near the midsaggital line.

The internal uterine anatomy consists of a single common lumen without IUCs. This simple internal anatomy is a unique feature of this subfamily and distinguishes the stenodermine uterus from all other simplex forms. The loss of IUCs is considered a continuation of uterine fusion involving the internal lumina and, as such, is considered a synapomorphy of the subfamily. In the absence of IUCs, blastocyst implantation must occur in the common lumen. It has been reported that implantation in *Artibeus jamaicensis* occurs in the fundic end of the common uterine lumen (Wislocki and Fawcett, 1941; Fleming, 1971). Likewise, we observed implantation in this region for all specimens that possessed blastocysts or embryos. These included two *Centurio senex*, one *Sturnira lilium*, one *Ectophylla alba*, and one *Ariteus flavescens* (Fig. 8). In all cases, the initial site of implantation was in the extreme fundic end of the uterine lumen (blastocyst orientation could not be determined except for *Ariteus*, see Fig. 8).

## OVIDUCTAL HISTOMORPHOLOGY

### General Description

An excellent description of oviductal histomorphology can be found in Nilsson and Reinius (1969), whose terminology was followed in the present study. The oviduct is a tubular organ composed of three histologically well-defined tissue layers. An outer serosa is continuous with the peritoneum and joins the mesosalpinx to support the oviduct. A middle muscularis is comprised of
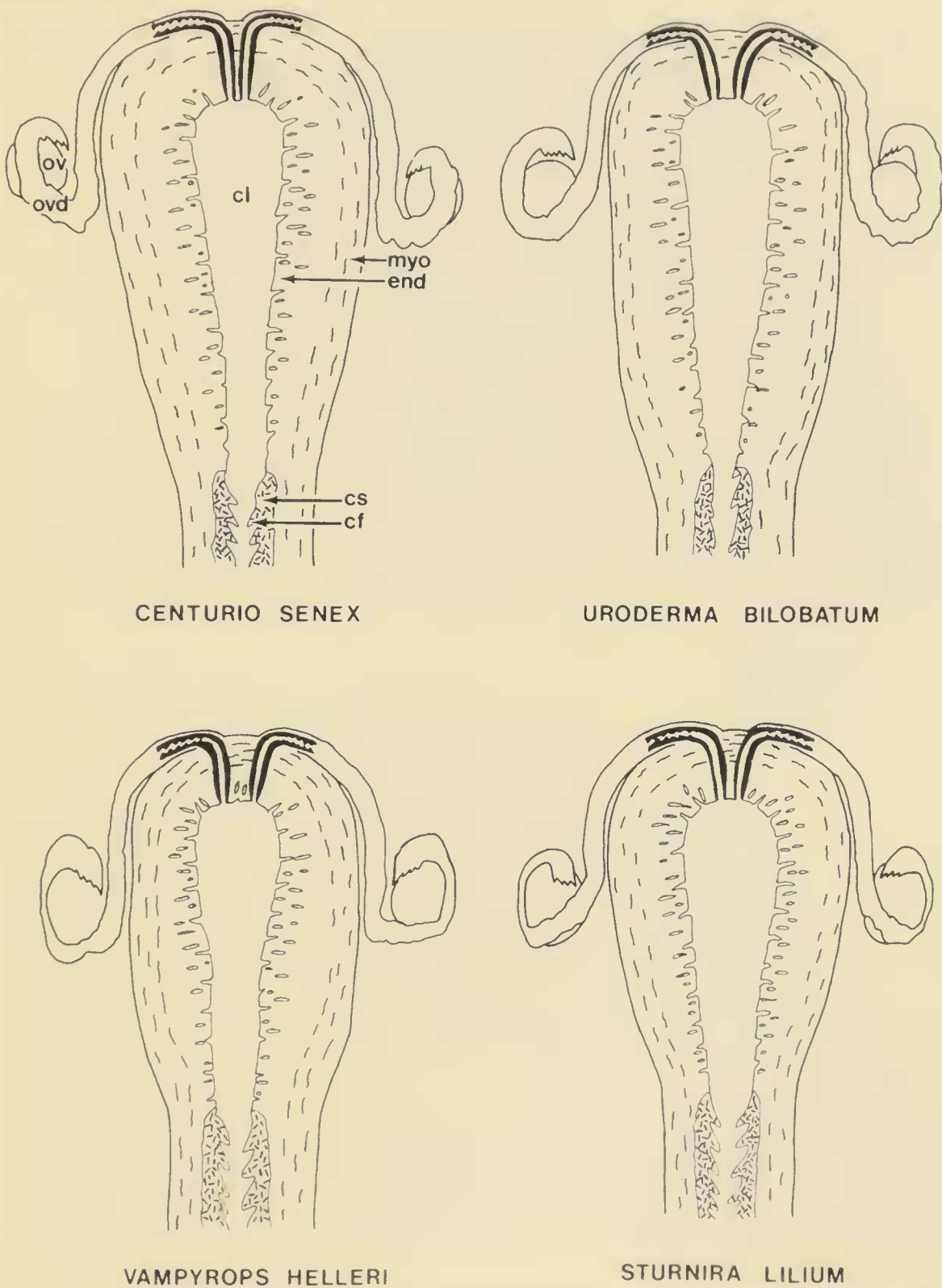
FIG. 7.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative Stenoderminae, including *Centurio senex*, *Uroderma bilobatum*, *Vampyrops helleri*, *Sturnira lilium*. Abbreviations can be found in Fig. 1.

circular and longitudinal smooth muscle layers and constitutes the bulk of the oviductal wall. The third and innermost tissue layer is a mucosa of simple to pseudostratified columnar epithelium with an underlying connective tissue (lamina propria). The oviductal epithelium undergoes marked histological changes dur-

FIG. 8.—Photomicrographs of the uterus and oviducts of a specimen of *Ariteus flavescens* (serial sections viewed frontally). *Top:* Oviducts descend through the fundus on the midsaggital line. *Bottom:* several serial sections later, a blastocyst is found implanted in the fundic end of the common uterine lumen. Orientation of the inner cell mass was towards the oviduct ipsilateral to the developing corpus luteum. Both 50×.

ing the reproductive cycle. These changes include activation of secretory cells and development of cilia (Nilsson and Reinius, 1969). The lamina propria is heavily vascularized and acts as a

structural framework for the epithelium. This organization is well illustrated as the mucosa is thrown into lamina propria-supported folds. These folds occur throughout the oviduct, but may vary in size or number in some regions (Nilsson and Reinius, 1969; this study).

The oviducts of phyllostomoid bats are coiled and regionally differentiated as in most eutherian mammals and all out-group chiropteran families examined. Beginning at the infundibular end, the oviductal regions include a preampulla, ampulla, isthmus, and junctura (Fig. 9). For the purposes of this study, these oviductal regions constitute the free portion of the oviduct and are defined herein as the extramural oviduct.

That portion of the oviduct that passes through the uterine wall is referred to as the intramural junctura (Nilsson and Reinius, 1969; Rasweiler, 1974). This oviductal region possesses all the histologically defined tissue layers found in the extramural oviduct, but lacks a definitive serosa. The muscularis is relatively thick and becomes continuous with the smooth muscle fibers of the myometrium. This portion of the oviduct has been the subject of considerable study because it involves the uterotubal junction (UTJ; Lisa et al., 1954; Edgar and Asdell, 1960; Hafez, 1973b). The UTJ includes the intramural junctura and its opening into the uterine lumen (Hafez and Black, 1969). Although much of the research concerning the UTJ has been limited to domestic or laboratory mammals, available data suggest that this region has unique anatomical characteristics in some eutherian orders (Anderson, 1928; Lee, 1928; Hafez and Black, 1969).

The UTJ of bats has not been described in a comparative sense, although it has been discussed by several authors (Rasweiler, 1972, 1974; Karim, 1975; Mori and Uchida, 1980). Among the families and subfamilies of bats examined in the present study, the junction possesses considerable variation in form. In vespertilionids and molossids, the UTJ is a prominent colliculus, whereas it is a low papilla in rhinolophids, hipposiderids, and *Mystacina*, and a complicated, pocketed region in pteropodids and emballonurids (Fig. 1). In contrast, the UTJ in noctilionids, mormoopids, and phyllostomids has been markedly simplified. The lumen of the intramural junctura opens into the cornual lumen, IUC, or directly into the common uterine lumen without any oviductal or uterine elaboration (Figs. 2, 3, 4). The simple morphology of this region is regarded as a synapomorphy of the superfamily Phyllostomoidea. In the systematic accounts that follow, patterns of
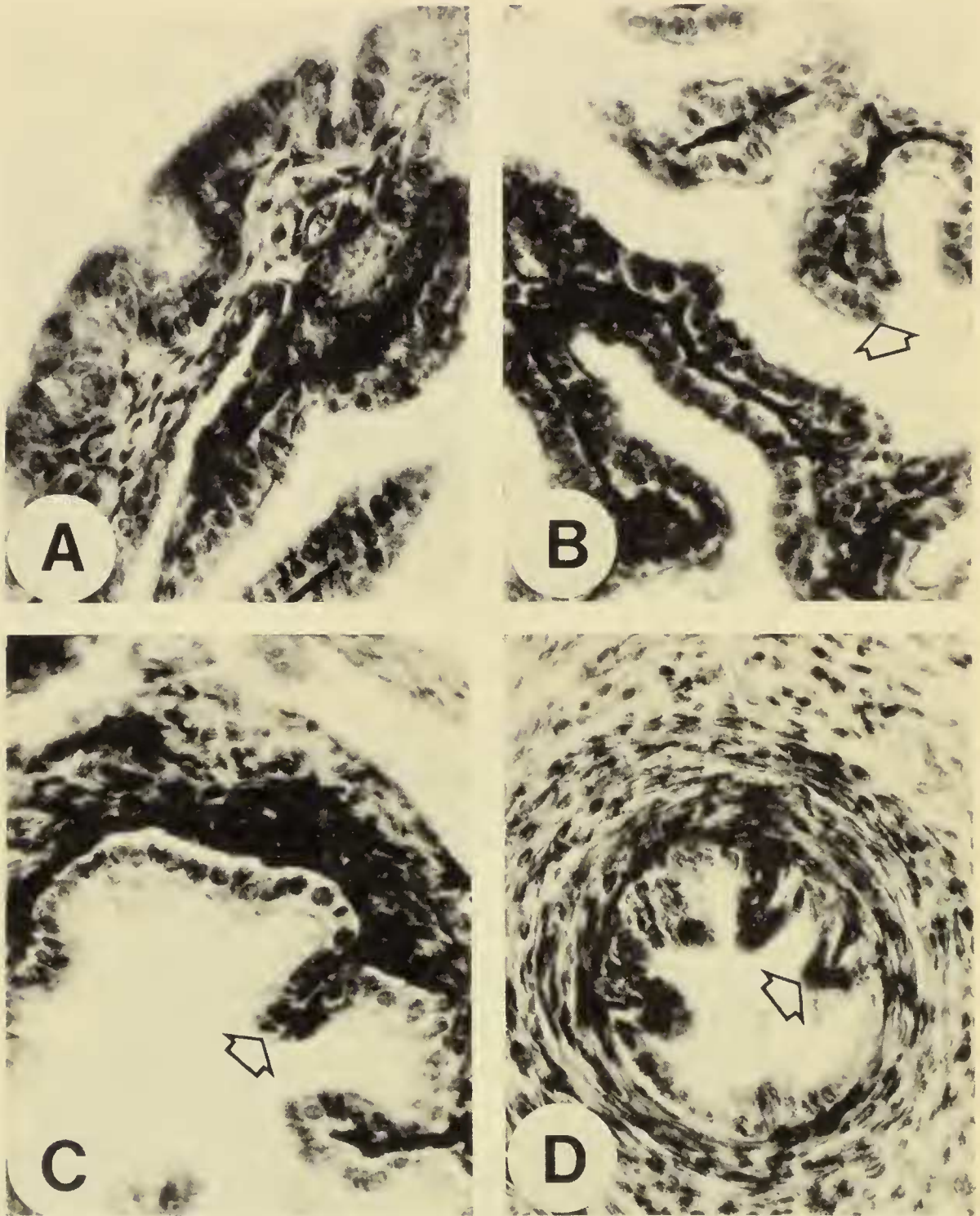
Fig. 9.—Oviductal histomorphology varies considerably among regions of the oviduct. This specimen of *Monophyllus redmani* was reproductively active, with a large corpus luteum but with no evidence of blastocyst or recent pregnancy. **A**, Preampulla with external folds (fimbriae) and high, cilliated epithelium; **B**, ampulla with prominent lamina propria-supported folds (arrow) and moderately high, cilliated epithelium; **C**, isthmus with relatively few, moderately low folds (arrow) but high, vacuolated epithelium; **D**, extramural junctura with narrow lumen and low folds (arrow) that usually lack lamina propria support and low, usually noncilliated epithelium. All photomicrographs 321×.

variation in oviductal histomorphology among phyllostomoid bats are illustrated and discussed.

## Family Noctilionidae

Specimens of *Noctilio albiventris* and *N. leporinus* examined in this study possessed the same qualitative features of oviductal histomorphology. The oviduct of *N. albiventris* has been described in detail by Rasweiler (1977, 1978) and we confirm his observations.

The extramural oviducts enter the uterus at the apical tip of the cornua (Fig. 2). Just outside this entry the oviduct is reflected laterally, so that the extramural oviduct overlays the cranial end of the uterine cornua. This arrangement is similar to that observed in other bicornuate phyllostomoids and out-group chiropteran families (Figs. 1, 3).

The intramural junctura is a short segment which passes through the uterine wall and opens into the cornual lumen. A dense lamina propria supports prominent mucosal folds. These folds line the intramural junctura throughout its length to the UTJ (Figs. 3, 10). The UTJ is simple compared to the chiropteran out-groups examined; it opens into the cornual lumen without elaboration. However, it is perhaps noteworthy that the intramural junctura appears to empty into the internal cornual lumen somewhat below its apical tip (Fig. 3). This feature may represent a different mode of oviductal entry, or it may simply reflect the hypertrophied antimesometrial walls of the noctilionid uterus.

Rasweiler (1977, 1978) described a dramatic unilateral oviductal reaction in *Noctilio albiventris*. Under the influence of the active ovary, the ipsilateral oviduct is preferentially stimulated to secretory activity. The accumulation of glycogen and cytoplasmic vacuolation in oviductal epithelium may be controlled by local vascular pathways (Rasweiler, 1978). In the present study, specimens of *Noctilio albiventris* and *N. leporinus* that were preovulatory or with early-implanted blastocysts had hypertrophied, vacuolated oviductal epithelium. In all these specimens, branches of the ovarian and uterine arteries on the side ipsilateral to the active ovary were prominent and blood-engorged.

## Family Mormoopidae

The oviducts of *Pteronotus* and *Mormoops* are short, highly coiled, and regionally differentiated. Entry of the extramural ovi-
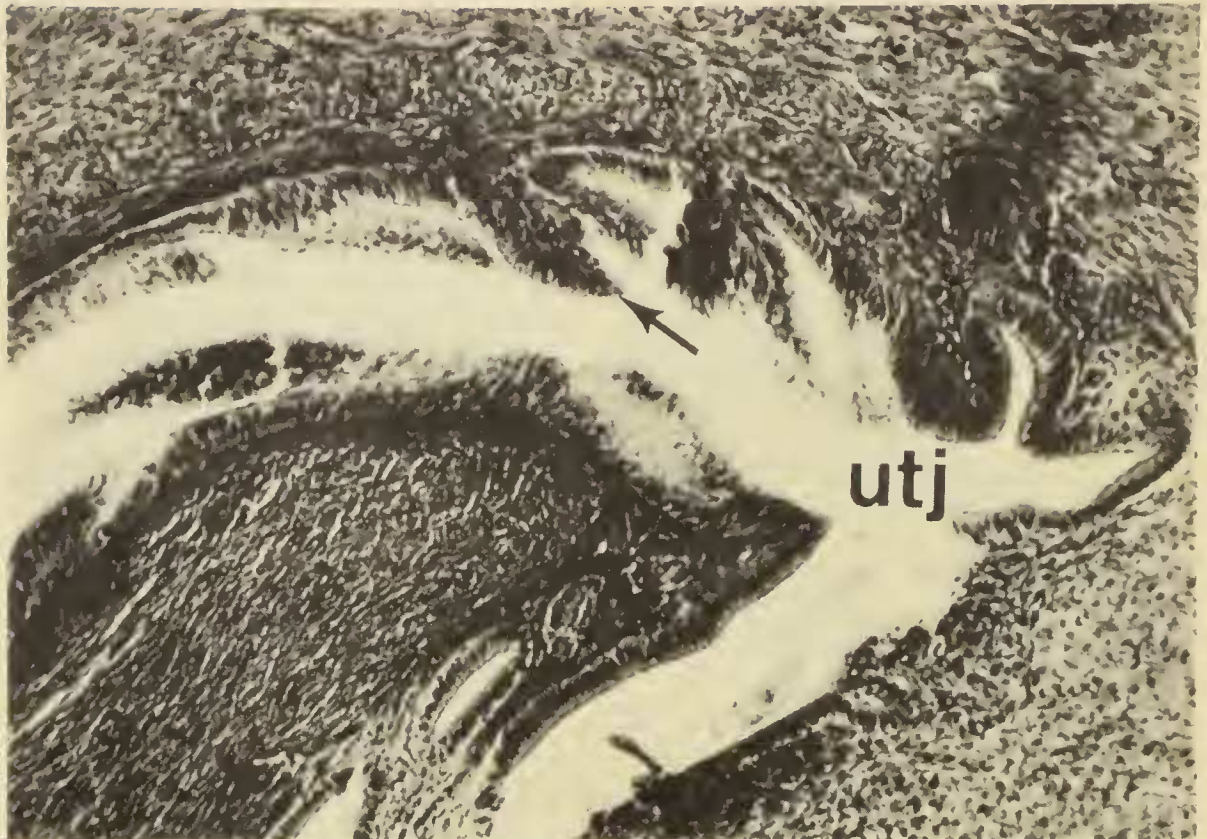
Fig. 10.—Photomicrograph of the intramural oviduct and uterotubal junction (utj) of *Noctilio leporinus* (frontal section). The oviductal mucosa has lamina propria-supported folds throughout the intramural junctura (see arrow). 279×.

duct occurs at the apical tip of the cornua as in other bicornuate phyllostomoids (Fig. 3). As in *Noctilio*, the extramural oviduct is reflected laterally, covering part of the cranial end of the uterine cornua.

The intramural junctura is a short oviductal segment that passes through the uterine wall and opens into the cornual lumen. At the UTJ, the oviductal lumen clearly opens at the extreme apical tip of the internal cornual lumen, an arrangement unlike that observed in noctilionids, but similar to that of *Desmodus* and the *Macrotus*-group. Mucosal folds are prominent throughout the intramural junctura and are supported by a dense lamina propria.

Available data on mormoopid reproductive physiology suggest that these bats are entirely right side dominant (Wimsatt, 1979). All specimens examined in this study confirmed this. In two specimens of *Pteronotus parnellii* that possessed early-implanted blastocysts, the right oviduct was preferentially hypertrophied. However, in nonpregnant, preovulatory specimens of *P. quadridens* and *P. macleayii*, both oviducts exhibited secretory ability. In addition, branches of ovarian and uterine arteries and veins were seen to course between the ovaries and uterus in specimens of all these taxa (Fig. 11).
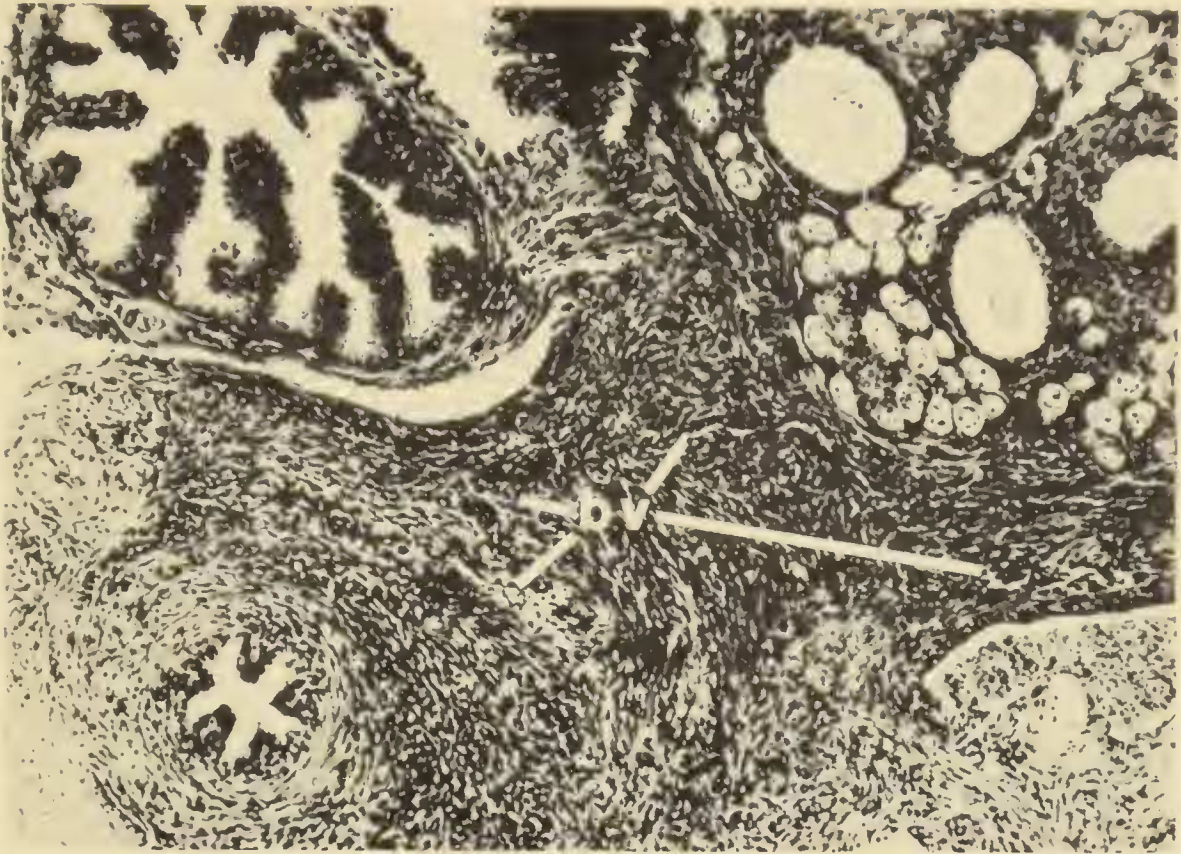
Fig. 11.—Photomicrograph illustrating uterine-ovarian relationships in a specimen of *Pteronotus macleayi*. Blood vessels (**bv**) were found between the active right ovary and the cranial end of the right uterine cornu. 378×.

## Family Phyllostomidae

Recent studies have detailed oviductal histomorphology in several phyllostomids, including *Desmodus*, *Glossophaga*, and *Carollia* (Rasweiler, 1972, 1974; Bonilla and Rasweiler, 1974; Quintero and Rasweiler, 1974). These studies suggest that phyllostomids share features of oviductal histomorphology with noctilionids and mormoopids.

Anatomical relationships between the uterus and extramural oviduct were found to be quite variable among phyllostomids. In those taxa that possess bicornuate uteri (i.e., *Desmodus* and the *Macrotus*-group), the extramural oviduct contacts and enters the apical tip of the cornua, an arrangement like that found in noctilionids and mormoopids (Fig. 3). On the other hand, phyllostomids with simplex uteri have a number of distinct forms of oviductal entry. In the *Phyllostomus*-group, the oviducts enter the uterine body on the lateral (mesometrial) border (Fig. 4), whereas oviducts in all other simplex forms enter on the fundic border (Figs. 4, 6). This fundic pattern of external entry shows considerable variation among phyllostomid subfamilies. The site of entry in glossophagines, brachyphyllines, and carolliines is more lateral than in stenodermines.

Although the extramural oviducts contact and enter the uterus on the fundic border in glossophagines, the site of entry is somewhat variable (Fig. 6). In *Lonchophylla* and *Leptonycteris*, the external entry is on the latero-fundic border of the uterus. On the other hand, the entry in *Glossophaga*, *Monophyllus*, and *Anoura* is more towards the midline. In all glossophagines examined in this study, the intramural juncturae pass through the uterine wall and open into the IUCs. Due to the more lateral site of entry in *Lonchophylla* and *Leptonycteris*, the juncturae in those taxa are far apart with a large mass of functional uterine tissue between the oviducts. In *Glossophaga*, *Monophyllus*, and *Anoura*, the more fundic site of entry allows the intramural juncturae to converge on the midline. As a result, a smaller amount of functional tissue is interposed between the oviducts. Features of oviductal histomorphology in brachyphyllines agree in all qualitative respects with those observed in glossophagines. The site of entry in both *Phyllonycteris* and *Brachyphylla* is on the latero-fundic border of the uterus. This site of entry is identical to that of *Lonchophylla* and *Leptonycteris* (Figs. 4, 6).

Both *Carollia* and *Rhinophylla* have extremely long, coiled oviducts. The external entry of the extramural oviducts in *Carollia* occurs on the latero-fundic border of the uterus, a site of entry similar to that illustrated in *Glossophaga* (Fig. 4). However, in *Rhinophylla*, the external entry is more towards the midline, thus similar to that observed in *Anoura*. The extramural oviducts of both genera turn laterally and travel along the fundic border of the uterus. Upon reaching the mesometrial border they descend along the sides of the uterine body where they encircle the ovaries. This arrangement is similar to that found in stenodermines. The intramural juncturae of both *Carollia* and *Rhinophylla* converge on the midline where they open into the IUCs. The site of external entry and pathways of intramural juncturae result in relatively little functional uterine tissue being found between the oviducts.

Oviducts of all stenodermines examined in this study were long and tortuously coiled. Although the external entry of the extramural oviduct varies to some degree among stenodermine taxa, the entry is very near the midsaggital line in all members of this subfamily. In some taxa (e.g., *Uroderma*, *Vampyrops*, *Vampyressa*, *Vampyrodes*, and *Ariteus*), the site of entry is well off the midline; in others (e.g., *Artibeus*, *Enchisthenes*, *Sturnira*, and *Ectophylla*) the site is closer to the midline. In the most extreme

cases (*Centurio* and *Ametrida*) the oviducts enter on the midline (Figs. 4, 5, 7, 12). As a result of a fundic external entry and the pathway of intramural juncturae, little uterine tissue is interposed between the oviducts. Functional endometrium was lacking in this region in all but two taxa (*Vampyrops helleri* and *Vampyressa pusilla*). In all other stenodermines, the interposing uterine tissue is limited to a dense connective tissue stroma.

Resolution of the primitive or derived nature of the lateral and fundic oviductal entries in phyllostomids with simplex uteri is not simple. There are no ontogenetic data available on the development of the phyllostomid simplex uterus, and out-group comparison cannot be readily applied to determine the polarity of this phylogenetic character. However, based on indirect evidence of comparative and ontogenetic studies of the simplex uterus in anthropoid primates and edentates, it appears that a lateral entry is most easily derived from a bicornuate uterine anatomy. In the absence of contradictory evidence, we propose that a lateral entry, as exemplified by the *Phyllostomus*-group, is primitive for simplex phyllostomids. With progressive uterine fusion, the oviductal junction moves towards the midsaggital line with the result that the fundic entry of glossophagines, brachyphyllines, and carolliines is regarded as a derived morphology. This progressive movement of the oviductal entry reaches its most highly derived form in stenodermines.

The phyllostomid intramural oviduct possesses several unique features. Mucosal folds, prominent in the intramural junctura of noctilionids and mormoopids, were notably reduced in all phyllostomids examined (Fig. 13). This reduction of mucosal folds begins in the extramural oviduct near the external entry and continues to the UTJ. The mucosal lining of some taxa shows low folds, but these are without a supporting lamina propria. Restriction of mucosal folds to the extramural oviduct is a unique feature among bats and is considered a synapomorphy of the family.

Unilateral oviductal reactions have been described in *Glossophaga*, *Carollia*, and *Desmodus* (Rasweiler, 1972; Bonilla and Rasweiler, 1974; Quintero and Rasweiler, 1974). In this study, these reactions also were observed in the oviducts of preovulatory and early-pregnant specimens of these taxa. Identical unilateral reactions (ipsilateral to the functional corpus luteum) were observed in preovulatory and early-pregnant specimens of the following phyllostomid taxa: *Phyllostomus discolor*, *P. hastatus*, *Monophyllus redmani*, *Leptonycteris curasoae*, *Phyllonycteris*

Fig. 12.—Photomicrographs of the uterus and oviducts of a specimen of *Sturnira lilium* (serial sections viewed frontally). *Top:* Extramural oviducts overlay the fundic end of the uterus before they descend on the midsaggital line. *Bottom:* This photomicrograph, taken several sections later, illustrates the descent of the intramural juncturae on the midsaggital line. Both 64×.
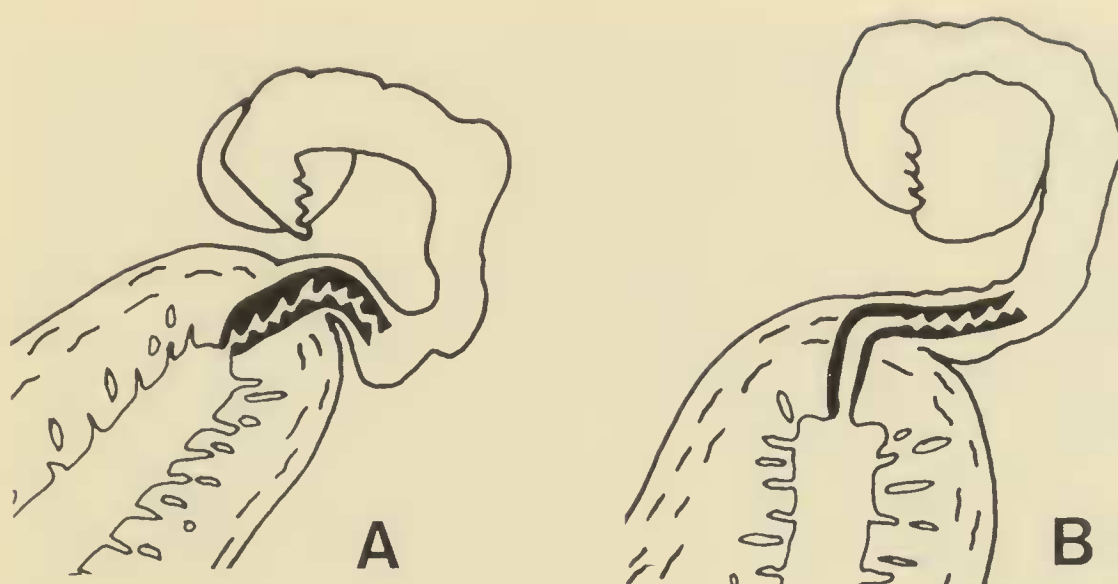
OVIDUCTAL FOLDS
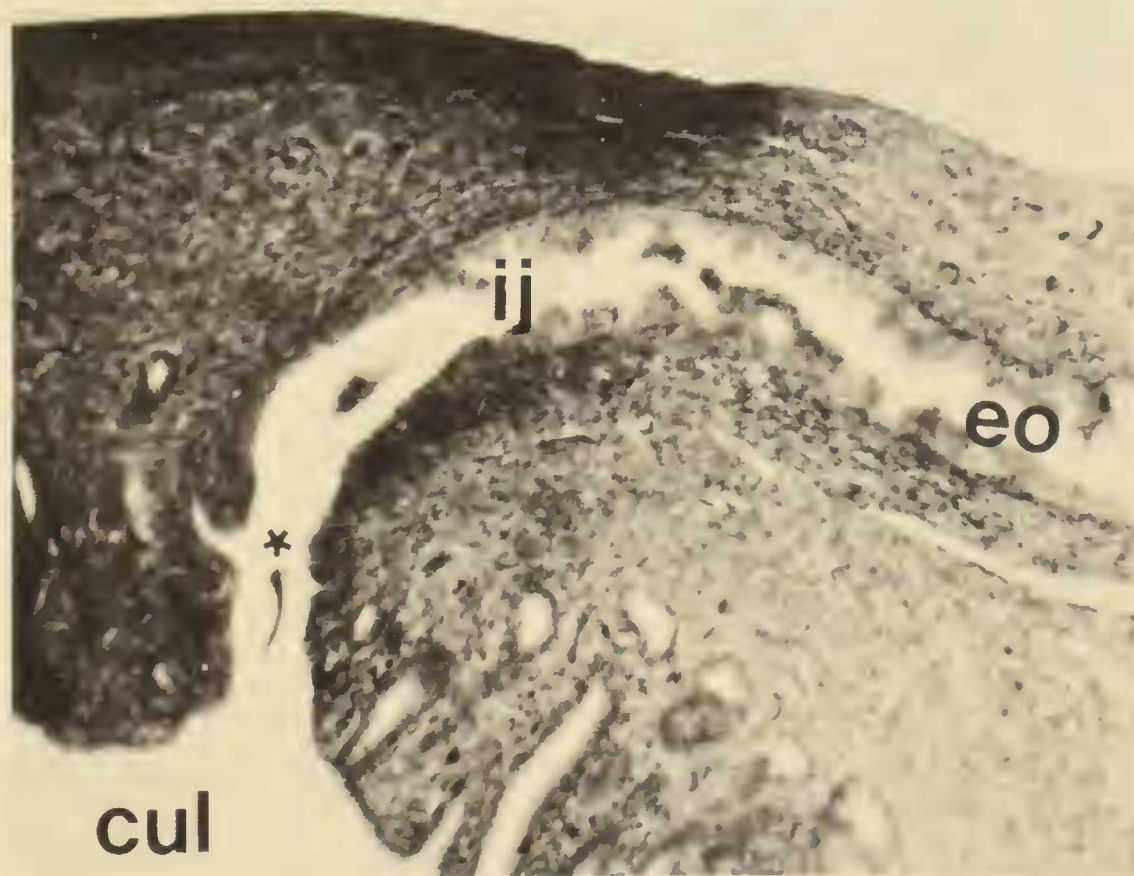PRESENT TO UTJ

FOLDS ABSENT
NEAR UTJ

Fig. 13.—*Top:* Diagram to illustrate oviductal mucosal fold character: **A**, mucosal folds present throughout oviduct to the uterotubal junction, as in noctilionids and mormoopids; **B**, folds lacking in the intramural junctura, as in phyllostomids. *Bottom:* Photomicrograph of the oviduct and uterus of *Glossophaga soricina* (frontal section). The oviductal mucosal folds are restricted to the extramural oviduct as in **B**, above. *Abbreviations:* **cul**, common uterine lumen; **ij**, intramural junctura; **eo**, extramural oviduct; asterisk indicates position of the intramural uterine cornu. 98×.

*aphylla*, *Ariteus flavescens*, *Artibeus jamaicensis*, and *Sturnira lilium*.

## OVARIAN HISTOMORPHOLOGY

Little is known concerning the comparative morphology of the ovary in phyllostomoid bats (Mossman and Duke, 1973). Rasweiler (1972) briefly commented on the ovaries of *Glossophaga soricina*. Likewise, Bonilla and Rasweiler (1974) noted interstitial tissues in *Carollia*. The most comprehensive study on ovarian morphology and histology of a phyllostomid was given by Wimsatt and Trapido (1952) for *Desmodus*. Ovaries of phyllostomoid bats examined in the present study were generally ellipsoidal to spherical in shape. Notable exceptions included mormoopids and the *Macrotus*-group, which have markedly flattened, atrophic left ovaries. In addition, both specimens of *Leptonycteris curasoae* had distinctly kidney-shaped ovaries.

Ovarian histomorphology in phyllostomoid bats is typical by eutherian standards. A cortex and medulla were readily identified in all phyllostomoids examined; the cortex contained primary follicles and a dense connective tissue stroma, whereas the medulla contained maturing follicles, corpora lutea, and numerous blood vessels. In most phyllostomoids, primary follicles are distributed throughout the cortex. However, in *Glossophaga soricina* and *Leptonycteris curasoae*, these follicle types are limited to the medial and lateral aspects of the ovary, respectively. It has been noted that polyovular follicles occur relatively rarely within mammals (Mossman and Duke, 1973; Harrison and Weir, 1977). In the present study, one young, nonpregnant specimen of *Ametrida centurio* was found to possess numerous polyovular follicles in both ovaries (Fig. 14).

Interstitial tissues are diverse; thecal and gonadal adrenal types were present in all taxa examined. In some taxa (e.g., *Carollia*) massive amounts of gonadal adrenal interstitial tissue were found in the mesovarium and ovarian hilus, observations identical to those reported by Bonilla and Rasweiler (1974). Mossman and Duke (1973:209) noted an unusual rete-type interstitial tissue in *Uroderma*. In the two specimens of *Uroderma* examined in this study, the rete epithelium was not active; however, several specimens of *Phyllonycteris* and *Carollia* did have hypertrophied rete epithelium.

The ovary and oviduct are generally suspended by the mesovarium and mesosalpinx which together form the ovarian bursa.

FIG. 14.—Polyovular follicles were found in both ovaries of a specimen of *Ametrida centurio*; these ranged in extent of development from small secondary to moderately large vesicular follicles. 240×.

Surprisingly, noctilionids, mormoopids, and phyllostomids possess a complex array of bursal arrangements. We will briefly summarize the bursal types observed among these families using the terminology of Mossman and Duke (1973). A partial bursal type with a laterally recurved oviduct and a medium to large peritoneal opening was found in Mormoopidae, *Phyllostomus*-group, Brachyphyllinae, and Glossophaginae (exclusive of *Anoura* and *Lonchophylla*; see below). As a variation, partial bursae with a medially recurved oviduct and a medium to large slit-like peritoneal opening were found in the *Macrotus*-group, *Desmodus*, and *Anoura*. On the other hand, a complete bursa with a medially recurved oviduct and a minute porelike or small slitlike opening was noted in *Lonchophylla*, Carolliinae, and Stenoderminae. *Noctilio* also possessed a complete bursa, but there the oviduct wrapped around the cranial end of the ovary.

The ovarian ligament extends from the ovary to an attachment at the junction of the oviduct and uterus. Comparative and ontogenetic studies have shown that this arrangement is a rather constant feature among eutherian mammals (Mossman, 1977). In the present study, this attachment was observed in all phyllo-

stomoids except the Carolliinae and Stenoderminae (Fig. 15A). In these phyllostomid subfamilies the ovarian ligament does not attach in this manner, but is attached to the lateral (mesometrial) border of the uterus (Fig. 15B). This arrangement is quite independent of the mesenteries that generally suspend the reproductive organs. This modified site of ligamentous attachment is an apparently unique feature among mammals and therefore is considered to be a synapomorphy of these two subfamilies.

## DISCUSSION

Histomorphological features of the uterus, oviducts, and ovaries in the New World bat families Noctilionidae, Mormoopidae, and Phyllostomidae illustrate a pattern of synapomorphy suggesting that phyllostomoid bats share a common evolutionary history. It is striking that extensive evolution of uterine morphology has occurred in these closely related families, compared to the conservatism found in most eutherian orders (Robin, 1881; Wood Jones, 1917; Matthews, 1941; Mossman, 1977). Comparative anatomists and embryologists have generally accepted a "fusion hypothesis" for the evolution of uterine morphology. This hypothesis is based on morphological and ontogenetic data viewed from a framework of out-group comparison. The present study has documented histomorphological details of the female reproductive tract in 29 genera and 36 species of phyllostomoid bats. Derived character states were hypothesized using out-group comparison. Phylogenetic relationships based on a cladistical analysis of the data presented in this paper are discussed by Hood and Smith (1982).

Wimsatt (1975, 1979) and Mossman (1977) have discussed at length some features of reproductive biology that apparently are correlated with uterine morphology. The most consistent correlation is found in litter size; mammals with short bicornuate and simplex uteri carry only one or a few young. However, bats represent a major exception to this correlation. The majority of chiropteran species, including those with duplex and long bicornuate uteri, produce and carry but a single fetus (cases of twinning are known for several families). Available data on noctilionids, mormoopids, and phyllostomids suggest that these three families are generally monovular and monotocous (Anderson and Wimsatt, 1963; Rasweiler, 1977; Bleier, 1979; Wilson, 1979). It seems clear, then, that the diversification of uterine morphology in phyllostomoid bats, and in the order Chiroptera as a whole, is not simply explained by adaptation towards small litter size.
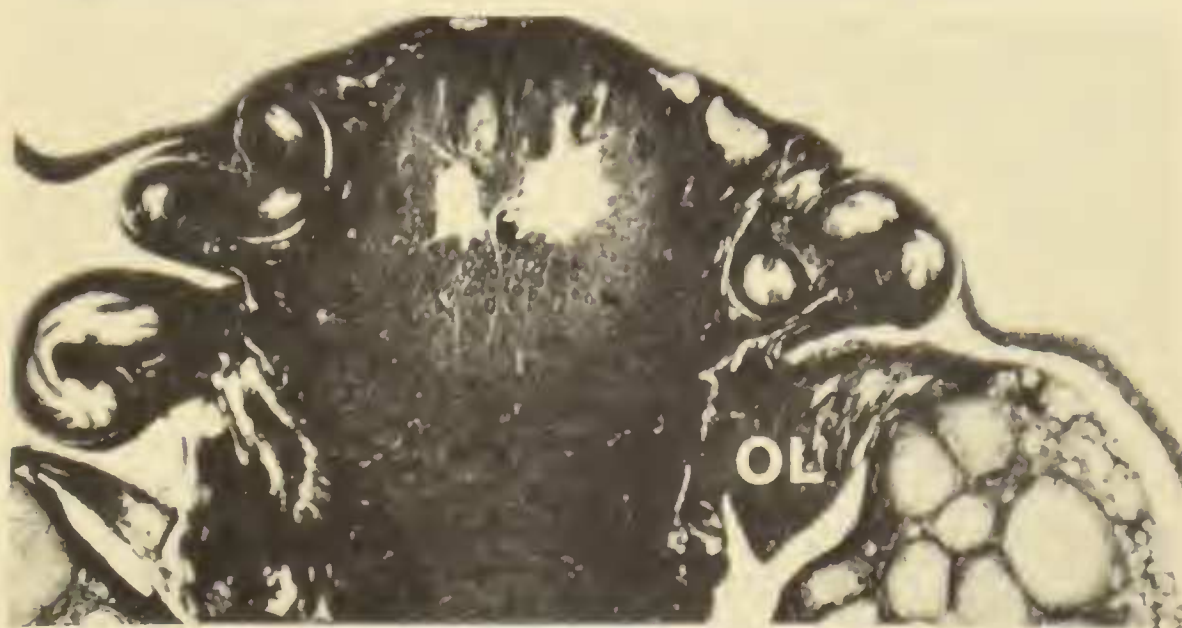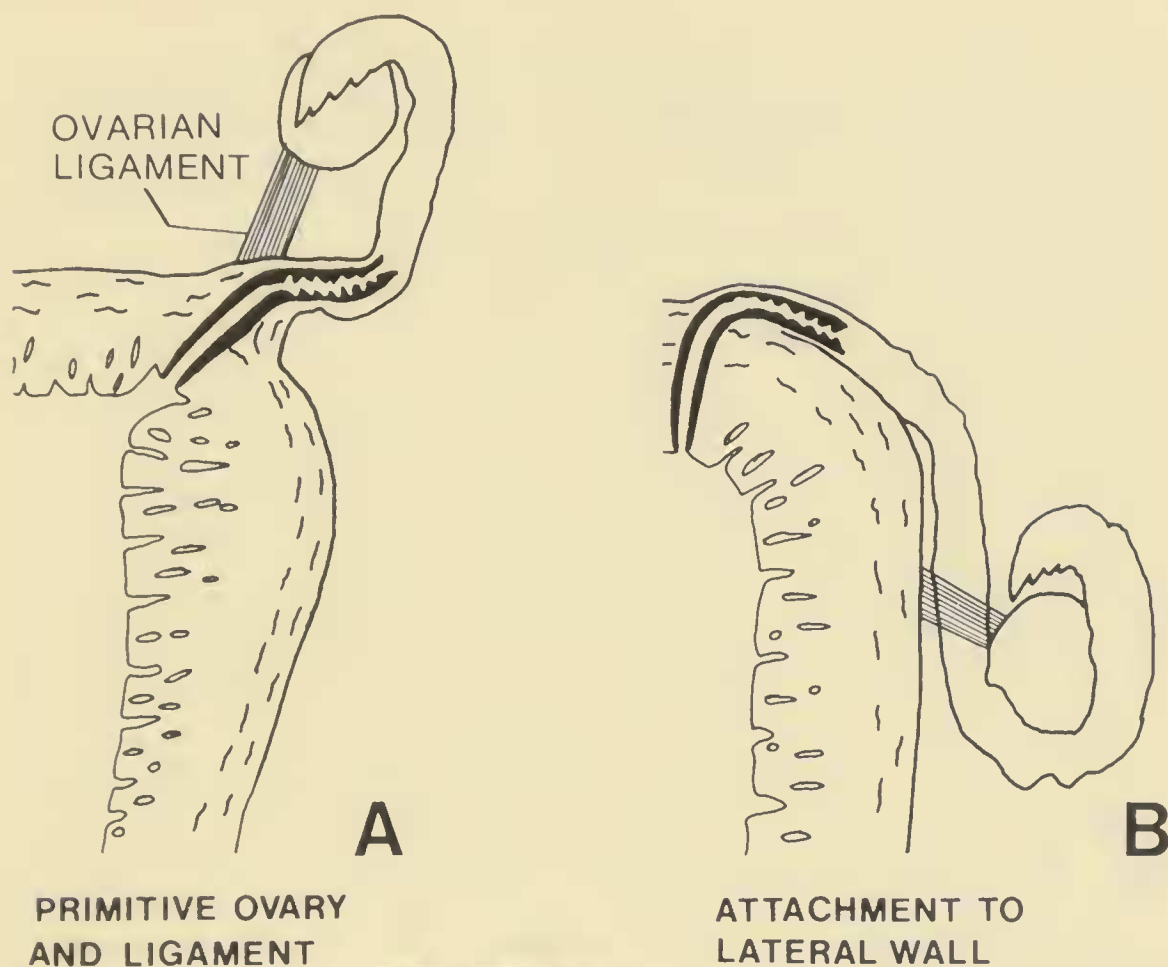
Fig. 15.—*Top*: Diagram to illustrate the ovarian ligament character: **A**, normal attachment between ovary and external entry of oviduct, as found in most eutherian mammals; **B**, modified attachment site, as found in carolliines and stenodermines. *Bottom*, Frontal section of the uterus, oviduct, and ovaries of *Vampyrops helleri*. The ovarian ligament (**ol**) extends from the ovary to an attachment site on the lateral (mesometrial) border of the uterus as in **B**, above. 10×.

*Reproductive Asymmetry and Unilateral Reactions*

Anatomical and physiological asymmetry is not known to be a major reproductive feature in eutherian mammals. However, in bats asymmetry dominates the reproductive strategies of several families (Wimsatt, 1979). Within phyllostomoid bats, mormoopids and the *Macrotus*-group are markedly asymmetrical (with right-side dominance). Details of mormoopid reproduction are virtually unknown and need to be examined. In the two *Pteronotus parnellii* that had early-implanted blastocysts, implantation occurred in the right horn and the corpus luteum was found in the right ovary. In contrast, a number of studies have been conducted on asymmetry in *Macrotus californicus*, which have shown that only the right ovary ovulates and the blastocyst always implants in the right uterine horn (Bradshaw, 1962; Bodley, 1974; Bleier, 1975). However, Bleier and Ehteshami (1981) demonstrated that when the right ovary is surgically removed, the left ovary can ovulate with subsequent development of early-implanted blastocysts in the left horn. These data suggest that expression of ovarian capacitance is complex and may be controlled by a number of factors. In the present study, the phyllostomine genera *Micronycteris* and *Trachops* have uterine morphologies similar to *Macrotus*. However, none of these specimens were preovulatory or pregnant; therefore, details of the reproductive cycle are unknown.

Unilateral oviductal and uterine reactions are known to occur in *Noctilio* and several phyllostomid genera (Rasweiler, 1978; 1979a). However, unilateral reactions are not unique to those families, but have been recorded in several species of Pteropodidae and Emballonuridae (Marshall, 1953; Gopalakrishna and Murthy, 1960; Gopalakrishna and Karim, 1971). Rasweiler (1978, 1979a) has hypothesized that local veno-arterial pathways mediate these reactions and that unilateral oviductal reactions are important in the prolonged oviductal development of preimplanted blastocysts. We observed unilateral oviductal reactions in our specimens of *Noctilio*, *Pteronotus parnellii* (but not in other mormoopids), and in several phyllostomids. Local uterine-ovarian vascular systems were observed histologically in all noctilionid and mormoopid taxa examined. The function of these remains unverified. Further studies on reproductive physiology in phyllostomoid bats would certainly benefit our general understanding of reproductive asymmetry in bats.

## Implantation

The process of blastocyst implantation has been reviewed by Wimsatt (1975) and discussed by Rasweiler (1979a). Sites of implantation are quite variable in bats. Initial implantation may occur anywhere in the gestational uterus of many taxa, although some bats have a restricted site of implantation at the cranial end of the uterine cornua (Rasweiler, 1979a). Among bicornuate phyllostomoids, blastocysts of *Noctilio* initially implant at the cranial end of the uterine cornua. In simplex forms, the intramural uterine cornua (IUCs) are further restricted sites. We confirmed these observations in our specimens of *Noctilio* and several phyllostomids and newly documented the function of IUCs in *Phyllostomus* and *Anoura*. On the basis of our histological observations (hypertrophied endometrium), IUCs can serve as primary sites of implantation in glossophagines, brachyphyllines, and carolliines. In stenodermines (which lack IUCs), blastocysts implant at the extreme fundic end of the common uterine lumen.

Orientation of the embryonic mass of the blastocyst at initial implantation is extremely variable in bats. In *Macrotus*, *Glossophaga*, and *Carollia* it is oriented towards the uterotubal junction (Rasweiler, 1977a; Luckett, 1980). We confirmed this and noted a similar orientation in several other simplex phyllostomid bats, including *Phyllostomus*, *Anoura*, and *Ariteus*. Blastocyst orientation has not been recorded in any mormoopid and in our material (two specimens), orientation of the mass could not be determined. The evolutionary significance of implantation and blastocyst orientation is not entirely clear; future studies on mormoopids and *Macrotus*-group phyllostomids are needed to clarify the general nature of these phenomena in phyllostomoid bats.

## Implications of Reproductive Histomorphology in Thyroptera

After the present study was completed, Wimsatt and Enders (1980) published a description of the uterus and placenta of *Thyroptera tricolor* (family Thyropteridae). They showed that *Thyroptera* shares derived uterine and placental features with noctilionids, mormoopids, and phyllostomids. From their account, it is clear that the uterus of *Thyroptera* is markedly fused externally, but has retained a relatively primitive internal uterine anatomy. Compared to phyllostomoid bats, external and internal uterine anatomy in *Thyroptera* is generally like noctilionids, although it appears that the thyropteran uterus may be somewhat more

derived than that described for *Noctilio*. In any event, we concur with Wimsatt and Enders (1980) that *Thyroptera* shares the synapomorphy—external uterine fusion fused—with phyllostomoids.

The uterotubal junction of the thyropteran oviduct was noted by Wimsatt and Enders (1980) as being simple. In the present study, this feature was considered a synapomorphy of the superfamily Phyllostomoidea. Although Wimsatt and Enders (1980) did not detail oviductal histomorphology, one of their photomicrographs (233:fig. 4) shows the oviduct to possess mucosal folds in the intramural junctura, an arrangement similar to that found in noctilionids and mormoopids. These observations support the inclusion of thyropterids in a monophyletic group including noctilionids, mormoopids, and phyllostomids.

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